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Absorption of atmospheric moisture by desert shrubs

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A large body of more or less conflicting literature has accumulated on the subject of the absorption of water directly from the atmosphere by leaves and other aerial parts of plants. The lack of agreement on this subject, and the fact that desert plants, if any, might be expected to take advantage of this means of adding to their meager water supply, led to an investigation of this subject by the writer, the results of which have appeared in the Botanical Gazette.* Briefly stated, they go to show that certain desert shrubs absorb to a limited extent water that is presented to their leaves and other aerial parts, while others under similar conditions are quite incapable of doing so.

At the time the experiments referred to were in progress no attempt was made to determine whether any of these plants are capable of absorbing water vapor directly from the atmosphere. It was thought that the low relative humidity of the region in which the Desert Botanical Laboratory is situated rendered such a process improbable, or, if it occurred, that it could hardly reach significant proportions. On returning to the laboratory, however, in the fall of 1905, it was learned that the ocotillo, *Fouquieria splendens*, a shrub which exhibits extreme sensitiveness to variations in water supply, and ordinarily casts its leaves in time of drouth, had been in full leaf during the entire summer, notwithstanding the exceptionally slight rainfall, the effects of which were

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* Spalding, V. M. Biological relations of desert shrubs. II. Absorption of water by leaves. Bot. Gaz. 41 : 262–282. 1906.

[The Bulletin for June 1906 (33: 327–365, *pl. 16, 17*) was issued 20 Jl 1906.]

plainly manifest in the dried-up and discolored vegetation around.* Various other species, notably *Parkinsonia microphylla*, *Lycium Berlandieri*, and some others, were also in full leaf, in striking contrast with their condition the year before; and this state of things, coupled with the extraordinary relative humidity, which for months had averaged approximately 60 per cent., as recorded by the hygrograph, suggested as a possible explanation of the long retention of their foliage the capacity of these plants to absorb water vapor directly from the atmosphere.† The prompt reaction of the ocotillo to increase of water supply, whether through root or stem, had already been strikingly shown by the fact that this species may form as many as five distinct leaf-coverings between February and August, "the exciting cause in each instance being an increase in the water supply" (through the root),‡ and also that leaf-formation may be induced in four or five days by artificial irrigation of the stem.§ It seemed worth while, therefore, to institute a special set of experiments in order to determine whether this shrub, and some others with which it is associated, are capable of directly absorbing and utilizing the water vapor of the atmosphere.

The method employed is essentially the same as that adopted in earlier experiments on leaf-absorption. Leaves and other aerial parts were accurately weighed and then kept for varying periods in a nearly saturated atmosphere, after which they were weighed and differences of weight noted.

The accumulation of more or less dew on one side of the receptacle employed in the experiments was taken to indicate a very nearly saturated atmosphere where the plant was placed. No deposition of dew on the surface of the plant was ever noticed, but if in any instance this occurred, the conclusion drawn from the results obtained is thereby strengthened.

Beginning with the ocotillo, two lots of leaves were taken, the first wholly green, though showing some loss of turgidity, while the other lot, from another plant, were turning pale, but had not become yellow. There was reason to believe that all were capable of photosynthesis, but that all had reached a condition in which more water could well be utilized. Inspection of the accompanying table (I), however, shows that both lots of leaves failed to gain in weight during two hours exposure to a nearly saturated atmosphere, and even lost slightly when kept in it over night. Moreover, following exposure to sunshine in the open air for some three hours, during which the two lots lost 0.6 and 0.8 per cent. of their weight respectively, they still failed to show any increase of weight after being kept nearly five hours in a practically saturated atmosphere. It is important, however, to note that in every case, during their stay in moist air, transpiration was reduced to such a degree as to amount essentially to complete suppression.

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* While the aggregate rainfall for 1905 was 23.18 inches, that for the six months, May to October, inclusive, was only 4.40 inches.

† CANNON, W. A. The effects of high relative humidity on plants. Torreya **6**: 21–25. 1906.

‡ CANNON, W. A. On the transpiration of *Fouquieria splendens*. Bull. Torrey Club **32**: 397–414. 1905.

§ LLOYD, F. E. The artificial induction of leaf-formation in the ocotillo. Torreya **5**: 175–179. 1905.

TABLE I. FOUQUIERIA SPLENDENS. OCTOBER 27–28, 1905.

No.	Time.	Weight.	Loss or Gain.		Conditions.
1	10.30 A.M.	9.257G			Weighed soon after gathering. Recorded relative humidity = 25 per cent.
2	10.35 "	10.677			Weighed soon after gathering. Recorded relative humidity = 25 per cent.
1	2.10 P.M.	9.236	0.021	Loss.	After exposure to currents of air in laboratory.
2	2.15 "	10.654	0.023	"	After exposure to currents of air in laboratory.
1	4.10 "	9.234	0.002	"	After exposure to nearly saturated atmosphere.
2	4.15 "	10.652	0.002	"	After exposure to nearly saturated atmosphere.
1	4.40 "	9.231	0.003	"	After exposure to open air of laboratory.
2	4.45 "	10.648	0.004	"	After exposure to open air of laboratory.
	October 28				
1	6.43 A.M.	9.225	0.006	"	After exposure to nearly saturated atmosphere.
2	6.50 "	10.637	0.011	"	After exposure to nearly saturated atmosphere.
1	10.42 "	9.167	0.058	"	After exposure to sunlight in open air.
2	10.33 "	10.558	0.079	"	After exposure to sunlight in open air.
1	3.33 P.M.	9.164	0.003	"	After exposure to nearly saturated atmosphere.
2	3.37 "	10.554	0.004	"	After exposure to nearly saturated atmosphere.

This experiment, agreeing with others not reported, indicates no capacity on the part of the leaves of *Fouquieria* to absorb water vapor, even after they have lost turgescence, or have turned pale and are almost ready to fall, but it does point to the prompt influence of a moist atmosphere, in checking, or even suppressing, transpiration, as the probably significant factor determining the long retention of its leaves the present year. At this writing, December 12, many individuals of the ocotillo have not been completely defoliated since last March.

In a second experiment with the same species, leafless shoots a

Table II. Fouquieria splendens. November 13–15, 1905.

No.	Time.	Weight.	Loss or Gain.		Conditions.
1	11.58 A.M.	3.858G			Weighed soon after cutting. Recorded relative humidity = 61 per cent.
2	12.05 P.M.	7.738			Weighed soon after cutting.
1	1.20 "	3.856	0.002	Loss.	After exposure to open air of laboratory.
2	1.24 "	7.735	0.003	"	After exposure to open air of laboratory.
1	3.29 "	3.868	0.012	Gain.	After exposure to nearly saturated atmosphere.
2	3.33 "	7.756	0.021	"	After exposure to nearly saturated atmosphere.
	Nov. 14.				
1	9.58 A.M.	3.886	0.018	"	After exposure to nearly saturated atmosphere.
2	10.04 "	7.785	0.029	"	After exposure to nearly saturated atmosphere.
1	12.54 P.M.	3.863	0.023	Loss.	After exposure to open air of laboratory. Recorded relative humidity = 45 per cent.
2	12.57 "	7.750	0.035	"	After exposure to open air of laboratory.
1	2.40 "	3.873	0.010	Gain.	After exposure to nearly saturated atmosphere.
2	2.45 "	7.768	0.018	"	After exposure to nearly saturated atmosphere.
	Nov. 15.				
1	9.55 A.M.	3.836	0.037	Loss.	After exposure to open air of laboratory.
2	10.00 "	7.712	0.056	"	After exposure to open air of laboratory.
1	12.34 P.M.	3.848	0.012	Gain.	After exposure to nearly saturated atmosphere.
2	12.40 "	7.734	0.022	"	After exposure to nearly saturated atmosphere.

few centimeters in length, with their terminal buds, were employed. Table II shows that these shoots gained appreciably in weight in a nearly saturated atmosphere, but rapidly lost more than they had gained when left in an atmosphere the relative humidity of which was registered at 45 and upwards. The experiment was varied by covering the buds of another shoot with vaseline and leaving those of a control shoot untouched. As shown by Table III, the former shoot gained in weight nearly two thirds as much as the control, thus indicating that although the buds share in the process they are not the chief absorbing structure.

TABLE III. FOUQUIERIA SPLENDENS. NOVEMBER 14–15, 1905.

No.	Time.	Weight.	Loss or Gain.		Conditions.
3	10.48 A.M.	5.643G			Weighed soon after cutting.
4	10.54	6.406			Weighed soon after cutting.
3	2.05 P.M.	5.655	0.012	Gain.	After exposure to nearly saturated atmosphere.
4	2.10	6.425	0.019	"	After exposure to nearly saturated atmosphere.
3	2.30	5.650	0.005	Loss.	After exposure to air of laboratory. Recorded relative humidity = 44 per cent.
4	2.33	6.417	0.008	"	After exposure to air of laboratory. Recorded relative humidity = 44 per cent.
	Nov. 15.				
3	10.09 A.M.	5.618	0.032	Loss.	After exposure to air of laboratory.
4	10.14	6.365	0.052	"	After exposure to air of laboratory.
3	12.46 P.M.	5.629	0.011	Gain.	After exposure to nearly saturated atmosphere.
4	12.50	6.380	0.015	"	After exposure to nearly saturated atmosphere.

But, notwithstanding the fact, thus fully established, that the shoots of *Fouquieria* absorb considerable quantities of water vapor from a saturated atmosphere, it seems entirely unlikely that in nature the leaves receive from the branches any appreciable amount of water as a result. One morning with the recording hygrometer registering the humidity at 72, the branches lost rapidly a large percentage of what they had gained over night in a nearly saturated atmosphere, and this was the usual, rather than exceptional, state of affairs; so that the rapidity with which the branches return to the air the water they have absorbed, even when the humidity is high, seems to preclude the assumption that any, or at least any considerable amount, is passed on by them to the leaves.

It appears, then, in the case of *Fouquieria*, that (1) the leaves do not, even under favorable conditions, absorb water vapor from the atmosphere ; (2) the branches are capable of such absorption, as are also the buds, though the latter are not more specially concerned in the process than the former ; (3) both shoots and leaves give off water rapidly, not only in a dry atmosphere but also in one of rather high relative humidity ; (4) as is well known, this process is checked or practically suspended in an atmosphere nearly or quite saturated with water vapor.

Herein, apparently, lies the explanation of the fact that in spite of the very scanty rainfall of the summer, the ocotillo has remained in leaf during so large a part of the present year. It is not due to absorption of water vapor from the atmosphere, although the relative humidity, during the period of observation, has reached the extraordinary average of approximately 60 per cent., but it is due to the fact that water, which with lower humidity would be given off, has been retained by the plant. While, too, leaf-formation may be induced, as shown by Lloyd, by artificial irrigation of the stems, but not, as far as the present study indicates, by absorption of water vapor from the atmosphere, there results, nevertheless, from a long period of high relative humidity what is apparently of greater advantage to the plant, namely, the retention, for months in succession, of leaves already formed and in condition for productive work. Had the plants been defoliated, as they must have been if lack of rain had been accompanied, as usual, by low relative humidity, even the maximum number of new leaf-coverings, reported by Cannon, if they could have been produced, would probably fall far below the single continuous leaf-covering in productive energy, though this is a matter the settlement of which would involve another and very different line of experimentation.

Experiments similar to those already described were next carried out with *Celtis pallida*, which was remarkably fresh and green, notwithstanding the slight rainfall of the preceding summer. The leaves were found to lose weight rapidly in a dry atmosphere — upwards of 24 per cent. in three hours — and to gain extremely slowly in an atmosphere nearly saturated with water vapor — only eight-tenths to nine-tenths of one per cent. in five hours. Later, after abundant rain, fresh ends of branches, with leaves, lost 31 per cent. of their original weight when left in a desiccator over night, and subsequently gained in two hours barely enough to show that transpiration had been checked and absorption set up. After further drying, and consequent departure from natural conditions, the rate of gain became greater, but the experiments fail to furnish any satisfactory evidence of the absorption of water vapor from the atmosphere by the living parts of this plant before pathological changes have set in.

Experiments of the same kind with the creosote bush, *Covillea tridentata*, were carried on both before and after heavy November rains. The earlier experiments, in which branchlets and leaves that appeared pretty dry, but still normally active, were employed, exhibited a gain of nearly 1 per cent. in two and one half hours, and their surface showed a distinct increase in the stickiness which is due to the mixture of mucilaginous and waxy substances with which they are coated. Later experiments with leaves and shoots much washed by recent rains showed rapid loss of weight in a dry atmosphere, amounting in some cases to ten per cent., while after remaining in a nearly saturated atmosphere over night the gain was only from one-tenth to less than two-tenths of what they had lost.

These and other experiments with *Covillea* indicate on its part a very limited capacity for absorption of water vapor from the atmosphere. None the less such absorption does take place, and it seems highly probable that it is advantageous to the plant. Even if absorption is so slight as merely to balance, or materially reduce transpiration for a time, this may, at a critical period, prolong the life and activity of leaves that would otherwise succumb; and furthermore the spread of the waxy-mucilaginous covering over the leaves, which is manifestly favored by a high percentage of atmospheric moisture, must also materially aid in checking excessive transpiration. A period of high relative humidity, occurring as it did the past summer, coincidently with a prolonged period of light rainfall, would operate in both of these ways to prevent the premature loss of parts actively engaged in photosynthesis. It is apparently impossible, at present, to express these complicated relations quantitatively, but this by no means detracts from their importance in the economy of a plant, which owes its dominant position over wide areas not to a single advantageous structure but to a complex of successful adaptations.

Experiments of the same general character were conducted on *Prosopis*, *Parkinsonia*, *Franseria*, *Atriplex*, *Encelia*, and a number of other perennials which represent the characteristic vegetation of the region. To give these in detail would serve no useful purpose, and the results may be briefly stated as follows: The mesquite (*Prosopis*) absorbs water vapor through its leaves, but at a slow rate. *Parkinsonia microphylla* showed no capacity for absorption of water vapor except as the specimens employed retained their minute scale-leaves, and then only to a very limited extent. *Franseria deltoidea*, *Abutilon incanum* and *Encelia farinosa* all failed to show any gain whatever in a nearly saturated atmosphere until the experiments had been in progress from two to four days. Later some absorption took place, but up to the time when the leaves were plainly passing into a pathological condition the amount absorbed was wholly inadequate to compensate for what had previously been lost or even to restore turgescence.

From the hygroscopic action exhibited by the fronds of *Notholaena* sp., which in dry weather are rolled up, but are unfolded after rain, it was thought that they would probably exhibit some manifest capacity for absorption of atmospheric vapor, and this anticipation was realized, although, as the records show, it would take at least 14 days for the fronds under observation to absorb from a saturated atmosphere what they had lost in twenty hours, and keeping the curled-up fronds for days in a very moist atmosphere was not sufficient to induce their unfolding. Immersing in water was soon followed by their expansion, and partial unfolding was also induced by placing the subterranean parts in water. It appears, then, that with the coming of rain the fronds of *Notholaena* absorb water directly and that this is also accomplished, though with less prompt and complete unfolding, by the subterranean parts. As the plant continues to absorb water from the soil the fronds remain expanded until the water supply diminishes to a point where they begin to curl up. At this point a high percentage of atmospheric moisture would retard the process, thus keeping them unfolded longer than if the relative humidity were less, and maintaining them in an advantageous position for photosynthesis.

A review of the data gathered establishes the fact that of the twelve species of desert perennials subjected to experiment all exhibit some slight capacity for direct absorption of water vapor from the atmosphere, but in general the amount absorbed is inconsiderable in comparison with that given off in corresponding periods in dry air. As yet there is no evidence that these almost infinitesimal quantities of water are utilized in the body of the plant. The promptness with which the water thus absorbed is returned to the atmosphere suggests rather a superficial process, purely physical in its nature, and of no immediate physiological significance. In any case the present experiments, taken in connection with earlier ones already referred to, show that the net result to the plants found to be capable of absorbing either liquid water or water vapor is plainly much less in the latter than in the former case. Nevertheless, as shown most clearly in the experiments with *Fouquieria* and *Covillea*, a high degree of saturation of the atmosphere, by directly or indirectly preventing excessive transpiration, may be far more advantageous to the plant than a succession of light rains which are insufficient to moisten the soil; the advantage, in this case, being manifested in most striking fashion to the eye in the living green with which these otherwise sombre-hued shrubs of the desert are clothed.

Possibly the most important conclusion to be drawn from this study and a preceding one on leaf-absorption is the patent fact that the roots of desert plants constitute their only reliably active agent in providing a normal water supply. This conclusion, indeed, was to be expected; but it is none the less important to establish, in the face of evidence that might be interpreted otherwise, the capital fact that upon the roots of these desert plants rests practically the entire burden of securing and transmitting the water upon which they depend, and, however far some of them have departed from the habits of present-day mesophytes, they remain in this particular fundamentally unchanged.

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